Morphological basis for the waterproof characteristic of bird plumage

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Abstract: A surface variable, density of water-feather touching points (D_p) was proposed in this paper to express surface property of water repellency of contour feather. Tests in 29 species using breast contour feathers indicated that D_p was small in tericolous species, medium in wading and diving species, large in swimming species, with only a few exceptions. This implied that birds achieve appropriate D_p by optimizing the microstructure of feather to meet the requirement of water repellency. Therefore, D_p was a morphological marker linking structure and function of feather in studies of adaptive evolution of birds.

Keywords: Plumage; Water repellency; Rough surface; Microstructure; Water touching point density

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Introduction

Birds rely on air trapped in their plumage for thermal insulation. The plumage of aquatic birds must possess water-tight characteristic to avoid wetting the skin and losing heat when swim and dive. Although many studies have been conducted on water repellency of plumage for a series of aquatic species, it is still not fully interpreted. Keratin composing feathers is capable to absorb water. Consequently, feather can be soaked easily when bird is swimming and diving. Such characteristic can be changed if birds preen oil to the surface of feather. However, the removal of oil did not result in immediate soakage (Rijke 1968). Thus water repellency of feather is due to morphological properties to a great extent (Grémillet *et al*. 2005). The work of Cassie *et al*. (1944) on the wettability of porous surfaces highlighted that water repellency is linked to the surface morphological properties of feather. Studies on cormorants further proved this standpoint (Rijke 1968; Johnsgard 1993; Grémillet *et al*. 2005).

Rijke (1968) tried to link the water repellency with surface property of feather. He suggested that the water repellency of the feathers of ducks is greatly increased by a structural feature which can be expressed in terms of diameter and spacing of the barbs and barbules. This structural parameter is smaller for cormorant's feathers and causes a lesser extent of water repellency. However, this hypothesis conflicted with later findings that the plumage of cormorants was only partly wettable and keeping a thin layer of air while diving, balancing the antagonist constraints of thermoregulation and buoyancy (Elowson 1984; Wilson 1992; Grémillet *et al*. 1998). Critical penetration pressure (CPP), defined as the fresh water pressure required to cause penetration of a liquid through a body feather, was used to describe the capability of water resistance of contour feather (Elowson 1984; Stephenson *et al*. 1997; Grémillet *et al*. 2005). The partial wettability of cormorant plumage was explained that each body feather has a loose, instantaneously wet, outer section and a highly waterproof central portion. The outer, loosely structured part of both dorsal and ventral body feathers was completely permeable to water, while the inner part was highly resistant to water pressure. The CPP of inner section of great cormorant feathers was 3 times larger than that of some diving ducks (Grémillet *et al*. 2005). Such difference in water resistance between outer and central portion is undoubtedly due to the difference of their microstructure. However, the only knowledge heretofore linking feather structure and CPP is still the conception proposed by Rijke (1968), though the measures failed to interpret water repellency of cormorant feathers.

Morphologically, each barb on the rachis of a feather carries hooked (dorsal) barbules on one side and unhooked (ventral) barbules on the other, forming the vane through joints of hooked and unhooked barbules (Thomason 1923). Water repellency property of such structure should be determined by variables, like the density of water touching points, which are mainly contributed by both barbs and barbules. As proposed by Rijke (1968), space between adjacent barbs and barbules are variables determining the density of touching points. Our basic hypothesis is that swimming and diving birds require higher water repellency in their contour feather than terricolous species do. The parameter contributing to the surface property of feather might reflect such trends. Therefore, four surface property variables were calculated in all 29 species. The results proved touching point density at water-feather interface is correlated with behavior and of significance to address the strategy of water repellency.

Materials and methods

Breast contour feathers in 29 species were used, as shown in Table 1. Five contour feathers were sampled from each of five individuals in each species. All feathers were washed gently with neutral PH shampoo for human hair care and dried naturally after fully rinsed with deionized water. Structural variables of outer vane of each feather were measured under stereomicroscope and microscope by random sampling. They are 1) density of barbs (D_B) computed as the number of barbs per 1000 μm in the direction vertical to barbs, 2) Inter-barb space (S_B) was computed as reciprocal of D_B, 3) density of barbules (D_b) computed as the

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number of barbules per 1000 μm in the direction vertical to barbules, 3) length of hooked barbules (L_{hb}), 4) angle between barb and barbule (A_{Bb}), as shown in Fig. 1. Coefficient of barbule overlapping (C_b), defined as the multiples that L_{hb} divided by the length between adjacent barbs, was computed as $C_b=(L_{hb}\times \mathrm{Sin}A_{Bb})/S_B$. Density of water-feather touching points (D_p) defined as the number of points touching water within 1.0 mm^2 feather surface, was computed as: $D_p=D_B\times D_b\times C_b$. D_p of all species being studied were sorted in increasing order, and plotted in a histogram against species with known behavior. The position of species with given behavior was used to indicate the relatedness of structural variables and water repellency property.

Table 1 Species involved in this study

Order	Species	Behavior
Passeriformes	Eurasian jay (*Garrulus glandarius*)	Terricolous
	Dusky thrush (*Turdus naumanni*)	Terricolous
	Black-napped oriole (*Oriolus chinensis*)	Terricolous
	Melodious laughing thrush (*Barrulax canorus*)	Terricolous
Galliformes	Ring-necked pheasant (*Phasianus colchicus*)	Terricolous
	Black grouse (*Lyrurus tetrix*)	Terricolous
Strigiformes	Ural owl (Strix uralensis)	Terricolous
Falconiformes	Rough-legged buzzard (*Buteo lagopus*)	Terricolous
	Steppe eagle (*Aquila rapax*)	Terricolous
Ciconiiformes	Chinese pond heron (*Ardeola bacchus*)	Wading
	Median egret (*Egretta intermedia*)	Wading
Gruiformes	Demoiselle crane (*Anthropoids virgo*)	Wading
	Common crane (*Grus grus*)	Wading
	Black coot (*Fulica atra*)	Diving
Charadriiformes	Curlew (*Numenius arquata*)	Wading
	Pintail snipe (*Gallinago stenura*)	Wading
	Herring gull (*Larus argentatus*)	Swimming
	black headed gull (*Larus ridibundus*)	Swimming
	Common tern (*Sterna hirundo*)	Swimming
Procellariiformes	White-fronted shearwater (*Puffinus leucomelas*)	Swimming
Anseriformes	Spot-billed duck (*Anas poecilorhyncha*)	Swimming
	Mallard (*Anas platyrhynchos*)	Swimming
	Whistling swan (*Cygnus columbianus*)	Swimming
	Greater scaup (*Aythya marila*)	Diving
	Common pochard (*Aythya ferina*)	Diving
Pelecaniformes	Great Cormorant (*Phalacrocorax carbo*)	Diving
Podicipediformes	Great crest grebe (*Podiceps cristatus*)	Diving
Gaviiformes	Red-throated diver (*Gavia stellata*)	Diving
Sphenisciformes	Jackass penguin (*Spheniscus demersus*)	Diving

Results

Fig. 2a shows that most of the birds behaving wading (W), swimming (S), swimming and diving (SD) appear on the right side where D_B is higher, and terricolous species appear on the middle and left side where D_B is lower. But some wadding, swimming and swimming and diving birds also appear on the left side, intermixing with terricolous birds. This suggested D_B is a important component of the surface property for water repellency, but not very efficient. Similar results were also observed in D_b and L_{hb} (Fig. 2b, c). However, it is clearly revealed in Fig. 2d that swimming birds have the largest D_p, diving birds have medium D_p, and terricolous birds have the smallest D_p, although there is a few exceptions.

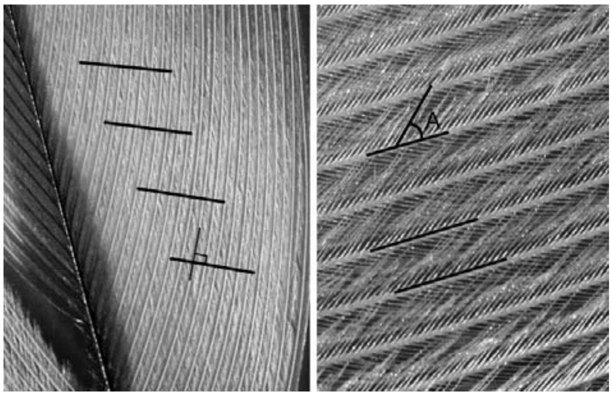

Fig. 1 Measurement of inter-barb space (S_B) or barb density (D_B) (left), inter-barbule space (S_b) and barb-barbule angle (A_{Bb}) (right)
SB or DB was directly measured as shown in left photo, S_b and A_{Bb} were directly measured as shown in right photo. Barbule density (D_b) was calculated as $(S_b\times \sin A)^{-1}$.

Discussion

As previously described, surface property for water repellency is determined by its roughness, saying the density of water touching points. For a contour feather, water touching points includes the shaft of barbs and dorsal edge of barbules including the base and pennulum. The higher density of barbs and barbules are in a contour feather, the higher water repellency it will have. However, D_B and D_b did not perfectly reflect such relationship as shown in Fig. 2a, b. A reasonable explanation is that feather is a multi-functioned organ, and its structural feature should meet various functional requirements synchronizingly, rather than singly for water resistance. There is, hypothetically, a trade-off in water repellency between barb density and barbule density. Lower D_B and higher D_b result in a suitable density of water touching points for water repellency, and vice versa. Jackass penguin has the highest D_B and medium D_b, but finally it returns the highest D_p, see Figure 2a, b and c. Another important factor influencing D_p is the length of dorsal barbules. A barbule covering more than one inter-barb space will doubtlessly increase the density of barbules due to its overlapping with barbules on next barb. Thus, C_b would be the proportion of increased barbule density. Therefore, D_p computed as the product of D_B multiplying D_b and C_b is more efficient to express water repellency property of feather than D_B and D_b singly. ·

Our result proved that terricolous species had lower D_p than water birds, coincidental with our previous hypothesis. But ring-necked pheasant is a special terricolous species having a D_p as high as swimming birds, see Fig. 2d. Such high D_p is mainly contributed by highly dense barbs (Fig. 2b). There was a sudden color changes at the top end of breast contour feather, which might be functional for ornamentation. Observation under stereomicroscope proved that whole of barb and barbules in this area had similar color, and the apparent color change was due to a sudden change of angle between barb and ventral (unhooked) barbules (Fig. 3). Barbules were comparatively short and sparse, thus small inter-barb space seemed essential to form such as structure. Therefore, high D_p is a secondary effect of ornamentation.

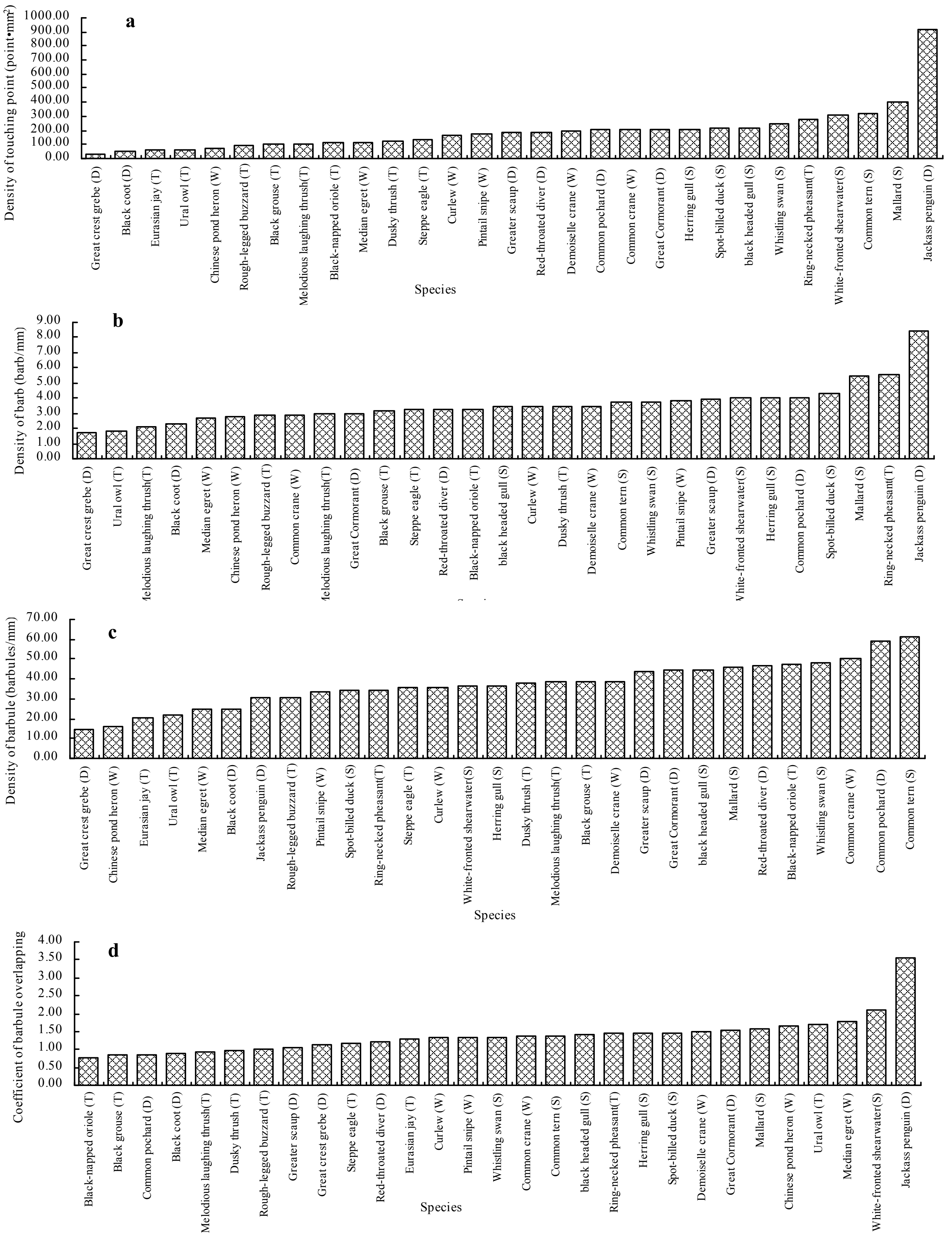

Fig. 2 Four surface variables of contour feather in 29 species of different behaviors

a. ; b. density of barbs; c. density of barbules; d. coefficient of barbule overlapping

T. terricolous; S. swimming; D. Diving; W. Wading

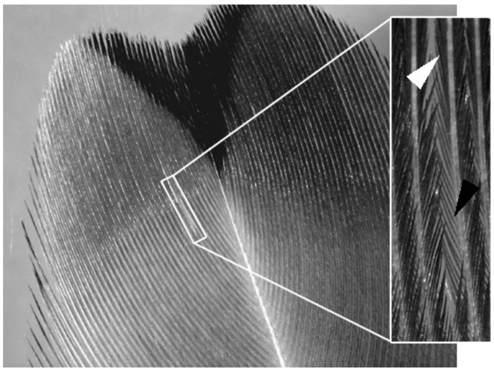

Fig. 3 Apparent color change due to a sudden change of angle between barb and ventral (unhooked) barbules (△▲) of breast contour feather of the ring-necked pheasant

Fig. 2a also demonstrates lower D_p in diving birds then in swimming species, except for Jackass penguin, suggesting the contour feather of diving birds have lower water repellency than swimming birds. This might lead to a conflict that diving birds require higher water repellency due to higher water pressure on the plumage surface than swimming birds when they are diving. High water repellency is doubtlessly essential for divers to prevent plumage soakage. However, they also require a thin, smooth and waterproof coat with no trapped air to reduce the positive buoyancy (Wilson *et al*. 1992). They achieve this by using muscles attached to the shaft of the feather to “lock down" the feathers to create a water-tight barrier (Kooyman *et al.* 1976). In addition, the feather rachis is flattened dorso-ventrally allowing it to bend and conform to the body shape readily with increasing water pressure for further squeezing air out. When they emerge back onto land the muscles re-erect the feather and provide a thick air-filled coat (Dawson *et al*. 1999). Diving species usually have contour feathers highly overlapped, thus the density of touching points on body surface will be multiplied. Therefore, medium D_p of single feather may result in sufficient water repellency property. Two extreme examples are great crest grebe and black coot. Their contour feathers have very low D_B, D_b and D_p, see Fig. 2, but are extremely overlapped, achieving a sufficient D_p when they are compressed.

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